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THE EXPRESSION OF SEXUAL DIMORPHISM IN HETEROSPOROUS SPOROPHYTES.*

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The writer has been engaged for a number of years in studying the evolutionary development of the higher plants. In the study of the flower, the problems of sexuality and of sporophyte dimorphism have presented themselves in an unusual manner, with many hints as to the nature of their hereditary expression.

The most remarkable dimorphism in plants is, of course, the difference of form and function expressed between gametophyte and sporophyte. One can hardly conceive of a more fundamental difference than exists, for instance, between the two generations of the ordinary ferns. In the higher plants this dimorphism is as extensive as sexuality itself. Sexual dimorphism seems more prominent to us only because we constantly associate our ideas with the sexual dimorphism of the higher animals.

Aside from the dimorphisms mentioned above there are also very striking vegetative dimorphisms which have no relation to sexuality or the alternation of generations. Such vegetative dimorphisms are usually expressed in different parts of the same individual. In plants like Megalodonta beckii (Torr.) Greene and Neobeckia aquatica (Eat.) Britt., the dimorphism is

*Contribution from the Botanical Laboratory, Ohio State University. No. 99.

related to the environment, the submerged leaves being dissected and the aerial leaves of the ordinary broad type, characteristic of closely related genera and species. In Lepidium perfoliatum L. there is just as abrupt and striking a change at the middle of the stem although there is no change in the surrounding medium. The lower leaves are finely dissected, while the upper are entire, oval in shape, and deeply clasping.

These dimorphisms are changes of states or expressions of hereditary units in the common tissue of a growing shoot. It is plain that they have to do with activity and latency rather than with the presence and absence or the shifting of hereditary units. This fact is to be kept in mind further on in the discussion of analogous sexual phenomena. Similar dimorphisms, although usually not so abrupt, are, of course, very general in great numbers of rosette plants. There are also cases where there is an abrupt, new development of shape, structure, and often color in the leaves just below the inflorescence. This type of vegetative dimorphism is especially common in the Euphorbiaceæ.

Among the fungi and many other organisms another type of dimorphism is common, which often involves not only the reproductive cells, but also the surrounding hyphæ. In the Ascomycetæ there is generally a decided difference between the conidial and ascus stages. These differences appear in different branches of an individual mycelium. The difference in sexual and nonsexual reproductive parts of such fungi corresponds to the vegetative dimorphisms mentioned above in that the phenomena are not associated with shiftings of the chromosomes. In some cases they are produced at rather definite stages of the life cycle, in others the change of expression depends on the environment.

Now what is meant by sexuality? In its simplest form it is a physiological difference expressed only in the developing sexual cells. As we go up the scale of plant complexity, we note that more and more of the tissues are involved until finally in the extreme forms the entire organism seems to be affected. From the evidence to be presented it must become apparent that in at least the vast majority of cases, and probably in all, the sexual condition is simply a state of the living substance which may continue for a greater or less length of time before a neutral state or the opposite sex condition is set up.

Physiological states may be due to chemical or other causes. Among the conditions in which organisms may be growing or living, the following may be mentioned: An active or quiescent state; vigorous or exhausted; sterile or fertile; immunity to disease at a certain age or susceptibility; specific diseased condition, like cretinism in children, or normal; gametophyte or sporophyte (without change of chromosome number); female or male; carpellate or staminate; juvenile state or mature state (like certain Acacias and Junipers); water form or air form; root state or stem state (usually with change of environment); conidial stage or sexual; protonema or scaly moss plant; difference of unusual morphological expressions without any hereditary difference, as for example, two or more very different types of insect galls on the leaves of celtis occidentalis L. In the case of the transition from gametophyte to sporophyte and vice versa, there is usually a change in the chromosome number which might be assumed to be the cause of the remarkable change in morphological expression, but there are many examples in both mosses and ferns, and also in the flowering plants, where the change takes place in the vegetative tissues without a shifting of chromosomes. The study of apogamy and apospory should shed much light on the nature of sexual and nonsexual states.

Before presenting the evidence in hand on the development of dimorphism in the heterosporous sporophytes a few general facts may be given in relation to sex as expressed in the gametophyte. The term sex used in its strict sense applies both to diploid and haploid individuals; among animals to diploid and among plants more commonly to haploid individuals, although there are numerous algæ in which the life cycle is essentially similar to that of the animals.

As already stated, there is a gradual development from a condition where no difference is apparent between the conjugating cells except the mutual attraction at a certain period to highly specialized cells, and further through hermaphordite organisms with strikingly different sexual organs on different parts of the same body up to completely unisexual individuals. In the past it has been assumed that sexuality was evolved because of some fundamental utility to the organism, but the doctrine of specific utility as an explanation of origins can have little place in the theory of any investigator who has carefully

studied the facts of plant evolution. The utilitarian view as developed to a supreme position in the Darwinian theory is largely discordant with present day views, but still seems to have a tenacious hold on the philosophy of sex. Things may be useful but the cause of their origin and persistence is another question. One can find endless cases where exactly opposite developments occur side by side in closely related species and varieties subject to a common environment. For example, note the barbed involucral bristles of Chaetochloa. In Chaetochloa verticillata (L.), Scrib. the barbs are retrorse while in the closely related Chaetochloa viridis (L.) Scrib. they point outward. In neither case have they any relation to seed distribution since the bristles remain on the dead inflorescence when the spikelets fall. In the genus Bidens, the papus awns are usually barbed, but here also some species have retrorse barbs and some outwardly projecting barbs. Since the awns are persistent on the fruit the retrorse barbs become useful but the others, if they have any effect must rather hinder seed distribution. In some species of Bidens the awns have no barbs whatever. Any number of similar cases could be cited.

Sex appears in some way to be associated with physiological and chemical states of the living protoplasm. It is perhaps most reasonable to assume, at present, that a certain organization or complexity of the cell is necessary before sexual states originate. But it is not true on the other hand that these states are necessarily set up at any stage of the life history even in organisms that have the essential complexity.

Among plant gametophytes the greatest sexual difference is shown in the Spermatophyta, between the male and the female. In the Archegoniata, very striking examples are certain species of Polytrichum where the mature male plant has a very different appearance in form and color from the female. The difference is much greater than is exhibited by many mammals or even birds. Now, just as in the gametophyte generation we find no vegetative dimorphism in the lower forms but find this becoming more and more pronounced as we ascend the scale, so also in the evolution of the sporophyte it is only the extreme forms in the evolutionary series that show but the one state throughout the entire individual. It is evident also that the gametophyte is far advanced in evolution

before the appearance of heterosporous sporophytes and that it shows complete sexual segregation from the Heterosporous Pteridophytes on up, while as stated, comparatively few sporophytes have attained complete individual dimorphism.

The gametophytes of Homosporous Pteridophytes exhibit both hermaphrodite and unisexual species, and in the case of certain unisexual ferns and horsetails, various experimenters have shown that the sex can be controlled or reversed after it is determined. The reversal can be brought about in either direction, but generally a much larger per cent. of females can be induced to produce male reproductive organs than males can be changed to females. This is probably due to the more specialized nature of the male soma, especially in relation to nutrition and vegetative growth. It is well to call attention here again to the fact that when the higher heterosporous plants developed definitely unisexual, gametophyte individuals, the segregation of the sexes was not accomplished in or by the reduction division, as one might have expected, but entirely independently of that process. All the four spores of a reduction division have the same sexual tendencies and all give rise either to male or to female gametophytes. Here the development of males and females is associated with the size of the spores. It is also interesting to note that in animals the spermatocytes through reduction give rise to four spermatids which develop into spermatozoa without any reference as to whether they contain an allosome or not. If the allosome is what determines sex, how is it that the two spermatids without allosomes develop maleness in exactly the same extreme way as the two which contain the allosome? Certainly the peculiar morphology of the spermatozoon must be considered maleness, if there is such a thing. The same reasoning would apply to the egg cell. In the case of the honey bee, all the oocytes develop eggs, which we certainly must admit is a female expression; yet these same eggs without fertilization change their sexual expression and develop into male individuals. In animals we cannot test out the hereditary qualities of the spermatozoa independently as we can the microspores of plants. If we could we would probably obtain results analogous to those coming from the androspores of certain species of Oedogonium, which give rise to dwarf males. In the higher plants than reduction of chromosomes has nothing to do with the maleness

and femaleness of the gametophyte. The determination of the sex takes place in the vegetative tissues of the sporophyte. Whatever it is that determines that the given tissue shall develop as a megasporophyll or a microsporophyll also determines absolutely the sex of the following generation of gametophytes. We are dealing with the establishment of a state in the cells of a vegetative tissue. A moment's reflection will show how extremely inappropriate is the application of the terms, homozygous and heterozygous in relation to sex individuals. Sexuality is just as pronounced in haploid gametophytes as elsewhere. The males, females and hermaphrodites of the higher plants can not be "zygous" at all in the normal life cycle. They are the results of segregation rather than of conjugation. The vast majority of sporophytes are bisporangiate and are of course homozygous or heterozygous in their chromosome condition, but here the sex is determined in the vegetative tissue before spores are produced.

In some species of Bryophytes it has been claimed that two of the cells of the reduction tetrad normally give rise to males and the other two to females. In such cases the sex must be determined in the spore mother cells (daughter cells of the sporocyte). But a sexual state might be influenced by unequal distribution of the cytoplasm. In great numbers of Bryophytes, however, the gametophyte is hermaphrodite and the establishment of the sexual state necessarily takes place in the vegetative cells of the gametophyte. Recently Allen* has reported a difference in size in one pair of chromosomes in the spore mother cells of Sphaerocarpos. Even if such a difference can be associated with a specific sex difference, it does not necessarily follow that the sex condition is determined by an irreversible sex factor in the given chromosomes. However, in this case where the sex individuals are haploid, such a hypothesis would be much more convincing than in the case of the diploid animals.

In dealing with sexual phenomena in plants, the problem is always complicated by the presence of an antithetic alternation of generations. Because of a confusion in terminology coming from a past period when the nature of the plant life cycle was unknown, it is often difficult to correlate the meaning of expressions used by different writers, especially of those who disregard

*Allen, Chas. E. A Chromosome Difference Correlated with Sex Difference in Sphaerocarpos. Science 46 : 466–467. 1917.

modern morphological discoveries. We cannot hope to analyze hereditary phenomena unless we have a correct understanding of the morphology and physiology of the parts under consideration. In recent years a consistent terminology has been developed by morphologists and there is no excuse for not using it. We have a sporophyte terminology and a gametophyte terminology. However, when applied to the new science of genetics out language is still inadequate, and one is immediately confronted with the difficulty of expressing hereditary phenomena in relation to sex when the sporophyte of heterosporous plants is involved. The homosporous sporophyte having no sexual dimorphism does not raise the issue, but when passing from homosporous to heterosporous sporophytes the problem presents itself with the common solution that organs formerly described and defined as without sex now obtain a radically different treatment, to the confusion of both the learned and the unlearned. It seems to the writer that the way out of the difficulty, at present, is to employ the sporophyte terminology when structures are mentioned, and to limit the sexual terminology, as far as possible, to the states or conditions of special gametophyte phenomena expressed in the sporophyte. Thus a spore bearing fern leaf is a nonsexual structure and a sporophyll of Marsilea is still nonsexual although it produces spores of two sizes. But the difference between the spores is a sexual difference. A carpel is still a megasporophyll and a nonsexual reproductive organ of the same fundamental nature as the megasporophyll of a heterosporous pteridophyte, but it is a sporophyll in which the sexual phenomena peculiar to the gametophyte are finding expression. The sexual state is thrown back, so to speak, into a small part of the sporophyte. It is this spreading of the sexual state, with an ever increasing area of the tissue involved, that constitutes one of the most interesting aspects of sporophyte evolution in the higher plants.

So far as the writer knows, Marsilea is the lowest living genus of heterosporous plants in respect to sexual dimorphism of the sporophyte. In external aspect the sporophyte shows no dimorphism, the sporocarps all being alike (Fig. 1). But the sporangia are slightly different, although the same in general shape. The most striking difference is in the stalks. The stalk of the microsporangium is comparatively long and slender,

while that of the megasporangium is short and thick. (Figs. 2 and 3). The dimorphism appears very pronounced in the spores. There is a remarkable difference between the microspores and megaspores in shape and size. There is here also the difference in spore development, in that the cells from the microspore tetrad all develop while only one of the cells of the megaspore tetrad develops. There is only one spore in the megasporangium in marked contrast to the large number in the microsporangium. Here then is a beginning of sexual dimorphism in the sporophyte. Now how is this difference in morphologic expression in the sporophyte tissue coming about? It is not by any shifting of chromosomes evidently; the tissues have a common vegetative origin side by side. The two kinds of sporangia do not even occupy different regions of the modified leaflet which bears them. It is the setting up of a differential condition of the same general nature as that which determines a dimorphic expression in the hard tissue of the sporocarp and the membranous tissue of the leaf blade on the same petiole.

Shattuck† found both in the normal plants and in all the cultures that a close examination revealed a homosporous tendency in that microspores were sometimes formed in the megasporangia, especially in those most distant from the nutritive supply. He also found that in cases of abortion in the microsporangia only one spore survives which is about sixteen times as large as the normal microspore. Shattuck discovered a method by which the nature of spore development in Marsilea can be controlled to a certain degree.

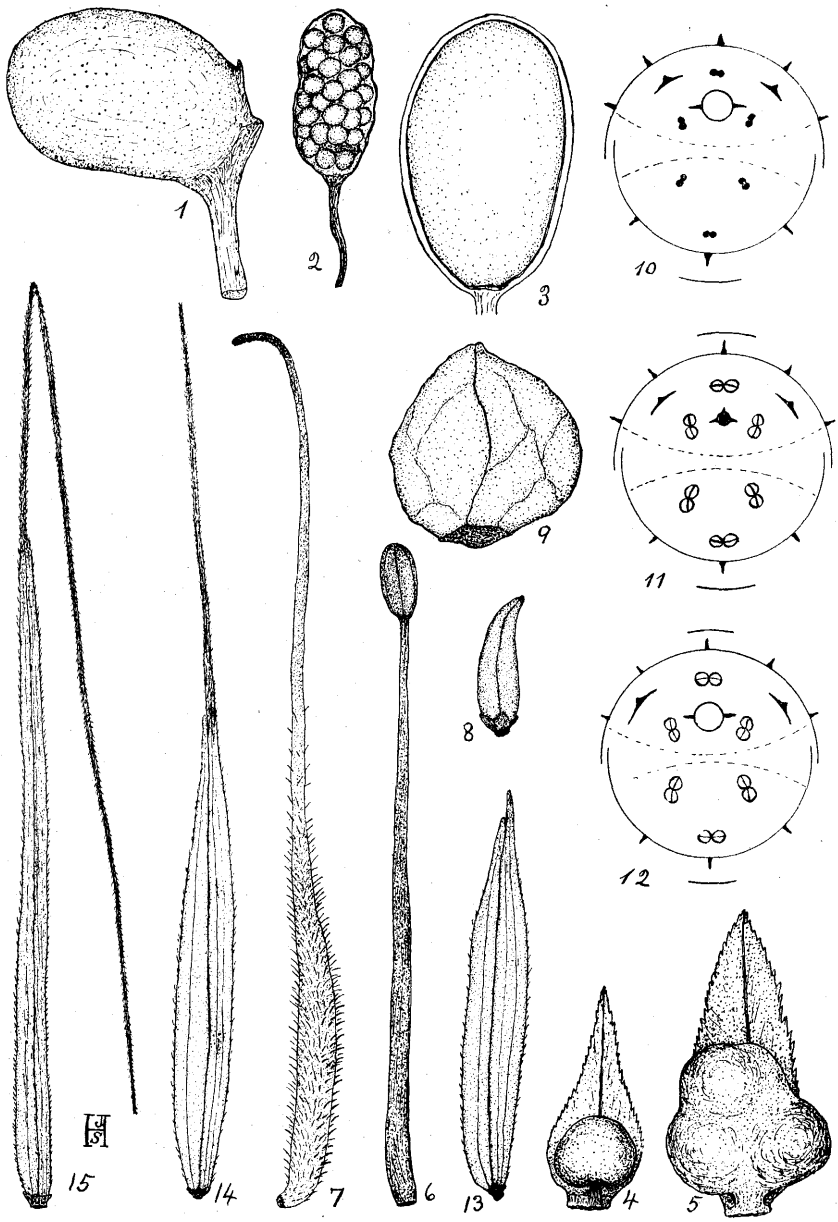
In the second stage of dimorphic advancement, as is well illustrated by Selaginella kraussiana (Kunze), the strobili are bisporangiate and each type of sporangium is confined to a separate leaf. There are definite microsporophylls and megasporophylls. In this species of Selaginella there is only one megasporophyll, at the base of the cone, to about twenty microsporophylls. The tissues which develop the two types of sporophylls are definitely located. Dimorphism of spores and sporangia is present as in Marsilea, but there are usually four megaspores. When we examine the blades of the sporophylls we also find a slight difference. They are both green and

†Shattuck, C. H. The Origin of Heterospory in Marsilea. Bot. Gaz. 49 : 19–40. 1910.

of the same texture, but somewhat different in shape and size. (Figs. 4 and 5). Here the dimorphic state has spread far beyond the spores and sporangia, until it affects the differentiation over a considerable area. The microsporangiate and megasporangiate states are set up in the incepts of the sporophylls. In the one case we have male determination, in the other female. Again, how is this determination brought about? By the activity and latency, whether only partial or complete, of hereditary factors. The sexual differentiation takes place before and outside of the phenomena of the reduction division and fertilization. It has absolutely nothing to do with segregation or association of chromosomes or allosomes.

In the gymnosperms generally the dimorphism is expressed not only in a difference in shape, size and structure of the sporophylls, but usually also in a difference in color; and since the cones are usually monosporangiate in the living species, the dimorphism extends to the floral axis or even beyond. But as all of these advancing evolutionary stages are also represented in the Anthophyta, no special consideration will be given here to the sexual dimorphisms of the gymnosperms.

When we come to the lowest Anthophyta, as in various genera of the Ranales, there is a considerable advance over the condition in Selaginella and related plants. Figures 6 and 7 represent a stamen and a carpel of Aquilegia canadensis L. The dimorphism appears in the shape, size and color of the sporophylls and in addition the megasporophyll shows that remarkable secondary sexual character, the stigma, which becomes necessary here because of the closed condition of the carpellate blade. The ovulary is also covered with prominent hairs while the stamen is smooth, a sex-limited character. In this case the sexual dimorphism expressed in parts of the sporophyte is about as great in character and degree as is usual for secondary sexual differentiations either of plants or animals. But the difference is confined to the sporophylls. The sporophyte as an individual shows but one form and nature and the dimorphism is developed in closely associated organs arising from a common tissue. The condition as represented by the flowers of Aquilegia canadensis L. is the normal state for the flowering plants. Indeed, if defined in general terms, the Anthophyta are plants with bisporangiate flowers with here and there groups or individual species which have advanced in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specialization to a greater or less degree toward the monecious or diecious state. In tracing from the bisporangiate to the monosporangiate flowers one finds a most remarkable display of vestigial structures, which are the result of suppression of the opposite hereditary factors by the distinctive sexual condition set up in the tissues from which they should develop. This inhibitory influence is of every degree of intensity in various species, ranging from cases where the organ is almost normal to its entire disappearance. In the more primitive, or rather less specialized species, reversions are very common.

The strictly diecious state is comparatively rare. There are no original monosporangiate flowers among the Anthophyta. The few examples, in which all vestige of a bisporangiate condition has disappeared, in nearly every case show a direct relationship to species or groups with the opposite structures present either as vestiges or in a normal condition. A few examples will be given to show the general trend of development to a typical diecious condition. It is well, however, to caution against the notion that the monecious condition is a step in the evolution of the diecious. It may be in some cases but mostly the development of diecious plants comes about directly through a succession of more extreme vestiges.

Sagittaria latifolia Willd., a low species of the Helobiæ and closely related to the bisporangiate genus, Echinodorus, is an example of a plant which has taken but a slight step toward the monecious condition. In typical cases the inflorescence bears

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EXPLANATION OF FIGURES 1–15.

Fig. 1. Sporocarp of Marsilea quadrifolia L.
Fig. 2. Microsporangium from the same.
Fig. 3. Megasporangium from the same.
Fig. 4. Microsporophyll of Selaginella kraussiana (Kunze).
Fig. 5. Megasporophyll from the same strobilus.
Fig. 6. Stamen of Aquilegia canadensis L.
Fig. 7. Carpel from the same flower, showing hairs on the ovulary, a sex-limited character.
Fig. 8. Staminate flower bud of Cocos nucifera L.
Fig. 9. Carpellate flower bud from the same inflorescence.
Fig. 10. Diagram of carpellate spikelet of Zizania aquatica L.
Fig. 11. Diagram of staminate spikelet from the same inflorescence.
Fig. 12. Diagram of a bisporangiate spikelet from the middle zone of the same inflorescence as Figs. 10 and 11.
Fig. 13. Staminate spikelet of Zizania aquatica L., showing lack of awn.
Fig. 14. Bisporangiate spikelet from the same inflorescence, showing awn of intermediate length.
Fig. 15. Carpellate spikelet from the same inflorescence as Figs. 13 and 14, showing long awn, a sex-limited character.

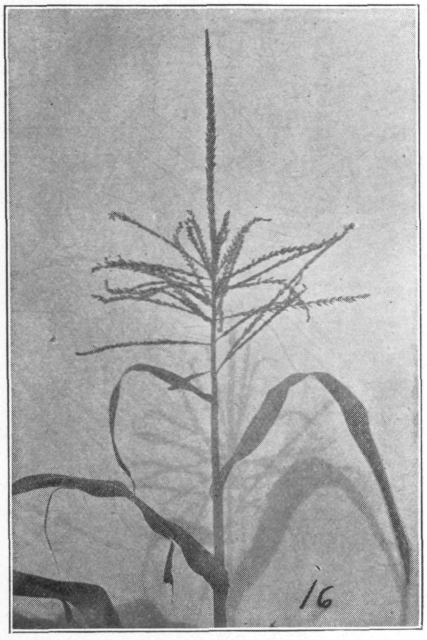
the carpellate flowers below and the staminate above on a common scape, although the entire inflorescence may be staminate or carpellate. There is not much difference in the corresponding perianth segments, but there is a difference in the receptacle. The staminate flower contains a half dozen or so of vestigial carpels whose imperfection would hardly be suspected unless compared with a normal carpel from a carpellate flower. The carpellate flower contains much more reduced vestigial stamens. In general, one can not predict which set of organs will be the more reduced in any given species though it is generally true that the carpellate flower is more apt to retain stamen structures than the staminate flower is to retain vestiges of the gynecium. This agrees with our notion that maleness in general is a more extreme condition than femaleness, but there are many exceptions like Sagittaria. As to the area involved in the dimorphic state, Sagittaria is rather extreme in that the inflorescence is divided into definite carpellate and staminate regions. However, there are many species of plants in which the two types of flowers are intermingled throughout the entire inflorescence. In the cocoanut, Cocos nucifera L., the flowers are monosporangiate and monecious. The diphorism of the flowers, which are situated on the branches of a large inflorescence, is very great. (Figs. 8 and 9). Both flowers have distinct vestiges of the opposite set of organs. The dimorphism extends out to the perianth. The sepals of the staminate flower are small and short, while those of the carpellate flower are large and cover the entire bud. The petals of the staminate flower are narrow while those of the carpellate flower are broad. Figures 8 and 9 are sketches of unopened buds drawn to scale and show plainly how the dimorphic condition is expressed in the tissues far beyond the sporangia. It is interesting to note that the vestigial carpels of the staminate flower are only slightly united, while those of the carpellate flower are completely syncarpous. The inhibitory staminate condition does not permit a complete union and a more primitive condition, apocarpy, is expressed. In the carpellate flower the stamen vestiges are small; however, one occasionally finds flowers in which one or more stamens are rather prominent. The writer discovered one case in which a vestigial stamen had developed a nearly perfect anther and the other five vestiges were larger than usual.

A further advance in the extent of the dimorphism is shown by those plants in which the distinctive staminate and carpellate flowers are confined to definite parts of the same inflorescence. A good example of this condition is the wild rice, Zizania aquatica L. This is a monecious species with the flowers in a large panicle. The upper part of the inflorescence is carpellate and the lower staminate. The change in condition usually extends transversely across the inflorescence axis and its branches. The staminate spikelets have a vestigial gynecium with three minute stigmas, while the carpellate spikelets have six distinct vestigial stamens. Here we have a considerable extent of tissue involving a large number of spikelets in the same sexual state. The amount of the vegetative tissue involved is much greater than in cases like the cocoanut. But the most striking peculiarity of this inflorescence is in the central part. Here the spikelets are bisporangiate having perfect stamens and gynecia. (See diagrams, Figs. 10, 11, 12). On the transition zone neither state is established and so no inhibition occurs. The sexual state is brought about in the sporophylls as is usual in bisporangiate plants in general as well as in the lower grasses. Examples like Zizania show plainly that the determination of staminate, carpellate, and bisporangiate flowers takes place in the vegetative tissues by the establishment of a certain physiological state and has nothing to do with gross or cellular morphology. The fundamental morphological conditions, both gross and microscopic, are the same throughout the entire panicle.

Zizania aquatica has also a remarkable sex-limited character. The lemmas of the staminate spikelets are awnless while those of the carpellate spikelets are long-awned. The bisporangiate spikelets in the neutral region have short awns. (Figs. 13, 14, 15). There is every gradation of length of awn in passing from the awnless lemmas of the staminate region to the long-awned lemmas of the carpellate region. No matter whether one or many awn factors are involved, the character of the awn is due entirely to the latency or activity of the awn factor or factors under the influence of the sexual state. Here then we have plain evidence of the nature of sex limited characters in plant sporophytes. Both awnless and awned lemmas have a common sporophyte heredity, but this heredity expresses itself in all degrees of latency and activity depending on the

sexual state of the tissue involved. If we hold to the reasonable hypothesis that the presence of a positive character is due to the presence of a factor or group of factors, then the absence of an awn on the staminate lemma is due to latency caused by the presence of the male condition in the given cells.

The relative position of the staminate and carpellate flowers in the inflorescence is reversed in various genera from what it is in the wild rice. In the aroids the staminate flowers are



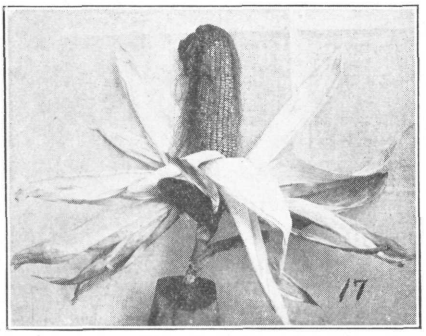


Fig. 16. Staminate inflorescence of Zea mays L.
Fig. 17. Carpellate inflorescence of Zea mays L.

usually above and the carpellate below. In the gama-grass, Tripsacum dactyloides L., the same is true and the two regions of the inflorescence show a very remarkable dimorphism. The lower part, containing the carpellate spikelets is remarkably modified. The dimorphism exists not only in the flowers and glumes but extends into the stem. The modified carpellate spikelets are enclosed in pockets, formed of highly modified joints of the stem which develops cleavage planes, the joints being separated at maturity, giving rise to very remarkable fruits.

The next step in the evolutionary progression of sexual dimorphism may be represented by Indian-corn, Zea mays L. Here as is well known the typical plant has a terminal staminate inflorescence, and one or more carpellate inflorescences developed from the side of the stem. (Figs. 16 and 17). The difference between the two branches is remarkable although they consist of the same morphological elements. The carpellate branch shows by far the greater deviation from the general vegetative morphology. The main differences are as follows:

Staminate stem.	*Carpellate stem.*
1. Normal internodes.	1. Internodes greatly shortened.
2. Normal sheaths.	2. Sheaths changed to husks.
3. Leaf blade normal.	3. Leaf blade absent or vestigial.
4. Inflorescence of comparatively primitive type, branched.	4. Inflorescence modified, with loss of branches.
5. Axes normal.	5. Axis a cob.
6. Character of glumes, membranous and elongated.	6. Character of glumes, chartaceous and broad.
7. Staminate flower.	7. Carpellate flower.
8. Little or no vestige of gynecium.	8. Remarkable development of style and stigmas (Silk).
9. Normal stamens.	9. Minute or no vestiges of stamens.
10. Microsporangia,	10. Megasporangia.
11. Microspores.	11. Megaspores.
12. Ordinary color in floral axis and glumes.	12. In some varieties, red or other color in floral axis and glumes.

The writer recently received an interesting ear of popcorn from Mr. L. E. Thatcher which shows a zonal arrangement of the sexual condition. This ear is a normal side ear with the lower part typically developed. In the middle is a complete zone, about an inch long, of staminate spikelets, while the outer part is typical ear structure again with normal grains. In this case there is a successive reversal of the growing axis. First the axis develops a cob with normal carpellate spikelets, then changes suddenly to a staminate condition and finally resumes its growth in the carpellate state.

The buffalo-grass, Bulbilis dactyloides (Nutt.) Raf. is a perennial, monecious grass with stolons which root at the nodes. According to Plank* and to Hitchcock† any given node produces but one type of inflorescence, and each kind of stolon is supposed to propagate its own kind. If this is true, the buffalo-grass would be an interesting plant for experimentation.

*Plank, E. N. Buchloe dactyloides Engelm. not a Dioecious Grass. Bull. Torr. Bot. Club. 19 : 303. 1892.

†Hitchcock, A. S. Note on Buffalo Grass. Bot. Gaz. 20 : 464. 1895.

The final step in the development of sexual dimorphism of the sporophyte is attained in the diecious condition. But here again some species are more definitely diecious. There are very few strictly diecious plants. Diecious sporophytes are isolated developments arising from parallel evolutions scattered from one end of the Anthophyte phylum to the other. In every instance they are derived from bisporangiate ancestors. In some cases as will be shown below the entire transition may occur in a single genus.

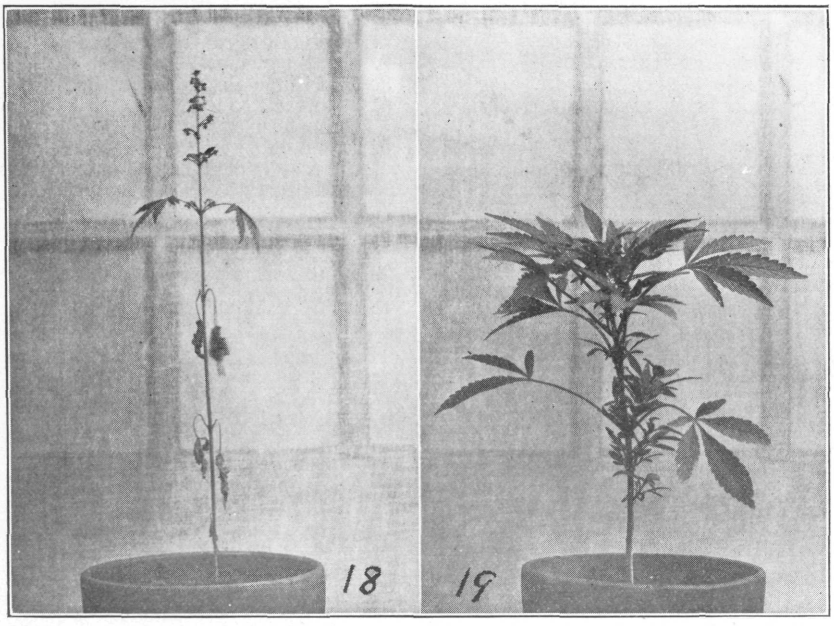


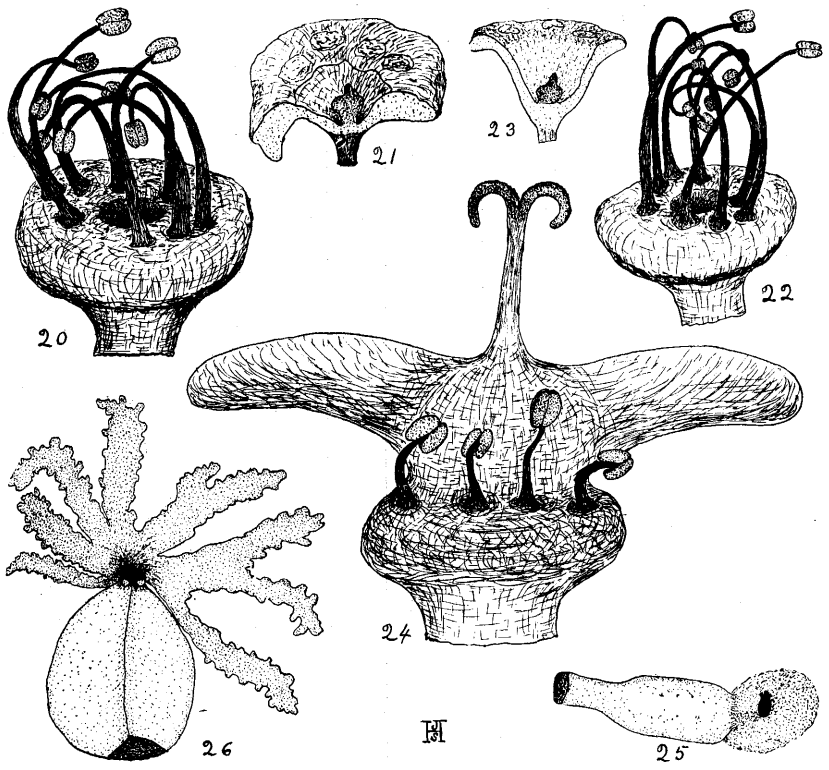
Fig. 18. A mature, dying, staminate plant of Cannabis sativa L., grown in the winter.
Fig. 19. A blooming, carpellate plant of Cannabis sativa L. of the same age as Fig. 18.

A good example of a diecious species is the common hemp, Cannabis sativa L. The plants are staminate and carpellate with other differences in the flowers besides the sporophylls. The carpellate plants are more robust and much longer lived. Figures 18 and 19 represent two plants of dwarf size raised in the middle of winter in the greenhouse. The plants photographed were transplanted to pots when mature. These abnor-

mal plants usually showed not more than five to seven leaf nodes, while plants raised in poor soil during the summer showed as high as twenty nodes. The staminate plant was dying of old age when photographed, although less than four months old. In plants like the hemp, the sexual dimorphism is as great if not greater than in the ordinary mammals. In fact, in many mammals it is much more difficult to recognize the sexes by somatic characters.

Among these hemp plants there were intermediates as is common in most diecious species. Staminate plants with more or less carpellate expression were considerably longer lived and more robust than those which were purely staminate. Not only did typical staminate plants sometimes produce bisporangiate flowers with more or less normal gynecia but some carpellate plants even produced stamens. This in spite of the fact that the plants were differentiated in their vegetative parts as typically carpellate. In plants grown later, out of doors, from the same seed no abnormalities were seen, but as the plants were not examined when they first began to bloom they may nevertheless have been present. The great abundance of intermediates in the winter, greenhouse plants was probably due to the abnormal environment, mainly a lack of light. The point to be emphasized in this connection is that we have here a diecious plant which shows sexual dimorphism even in its remote vegetative parts, but numerous individuals which are thus specialized have the ability to produce the opposite primary sexual generation and sexual cells, without any manipulation whatever being employed, except that they were grown in an unusual environment. How extremely impossible it would be in this case to claim that the specific sex characters were due to sexual Mendelian units, one individual being homozygous for sex and the other heterozygous. The whole behavior in these diecious plants is essentially the same as the sexual differentiation in the less extreme cases, traced above from Marsilea to Indian-corn. The maleness and femaleness represent states which inhibit to a greater or less degree the development of the opposite organs the heredity of which is potentially present, since both the staminate and carpellate plants do produce both male and female gametophytes. Dieciousness is a differential state, hereditary, of course, in the ordinary sense, which permits

under ideal conditions only the one set of spores and organs to be expressed, although the hereditary abilities for the other set are all present. The morphological expression is brought about in the same way as such a differential development takes place in the tissues of bisporangiate sporophytes, either with monecious or bisporangiate flowers.



Explanation of Figures 20–26.

Fig. 20. A staminate flower, with perianth removed, from a carpellate tree of Acer platanoides L.
Fig. 21. Part of the same flower, showing the vestigial gynecium.
Fig. 22. Staminate flower, wiih perianth removed, from a staminate tree of Acer platanoides L.
Fig. 23. Part of the same flower, showing the vestigial gynecium.
Fig. 24. Fruiting carpellate flower, with perianth removed, from the same tree as Fig. 22, showing normal young samara and vestigial stamens.
Fig. 25. Tip of a staminate flower of Rumex acetosella L., showing one of the six stamen filaments and the small vestigial gynecium with three minute vestigial stigmas.
Fig. 26. Gynecium from a carpellate flower of Rumex acetosella L., showing one of the three, large, branched stigmas, the other two being removed.

The genus Acer presents a very good series, passing from Acer platanoides L. through a number of species to Acer negundo L., the boxelder. So far as the writer's observations go, the boxelder is strictly diecious. Acer platanoides is in a much more primitive condition being but a short distance removed from the normal bisporangiate type. However the plants are staminate and carpellate. The writer has found carpellate trees which developed a few typical staminate flowers with vestigial gynecia and normally developed stamens, although the trees were covered with young fruit from the normal carpellate type of flower. (Figs. 20 and 21). Staminate trees were also discovered which were producing many carpellate flowers with vestigial stamens (Figures 22–24). These carpellate flowers developed normal fruit. Figure 24 represents a partially developed fruit. In both cases the percentage of the unexpected kind of flowers was small, but the staminate trees produced a much larger per cent. of carpellate flowers than the carpellate trees did of staminate flowers.

Rumex is another genus which begins with a partial bisporangiate state and ends in a diecious condition. Rumex crispus L. has bisporangiate flowers and carpellate flowers, the latter containing prominent vestigial stamens. Rumex acetosella L. is strictly diecious. The carpellate plant shows no vestige of the stamens or else these are too small to be seen without making special sections. But the staminate flower shows a small vestigial gynecium with three minute stigmas. (Fig. 25). The persistence of the three vestigial stigmas may be accounted for by the fact that the normal stigmas of Rumex are very large and branched. (Fig. 26). In some of the intermediate species of Rumex, as for example Rumex altissimus Wood, the vestigial stamens are rather prominent and the vestigial gynecium is of fair size with three small slightly branched stigmas.

A most striking example to illustrate the stages in the evolutionary development of dieciousness is presented by the genus Fraxinus. Fraxinus cuspidata Torr. has flowers with corolla and calyx. They are bisporangiate and very fragrant. Fraxinus quadrangulata Mx. has bisporangiate flowers, but no perianth. The merest vestige of a calyx is present. Fraxinus americana L. has a minute calyx and is strictly diecious. If the antiquated and misleading classification of the flowering

plants, still generally in vogue, could be eliminated, more botanists might realize the fact that monecious and diecious species are the extremes and commonly the culmination points of numerous parallel series rather than the first stages of Angiosperm evolution.

One more example will be given to illustrate the progressive differentiation of larger areas of staminate and carpellate tissues in an ascending phyletic series. In the Cyperaceæ the least specialized genera have bisporangiate flowers, like the genus Scirpus. Some of the species of this genus have a fairly well developed vestigial perianth of six segments. There are no special structures difficult to interpret. But in the genus, Carex, the perianth is absent and there is present the peculiar perigynium and other unusual structures. Carex is monecious; usually with staminate and carpellate flowers apparently without vestiges of the opposite organs. In Carex nardina Fries. the spikelets are all alike containing carpellate flowers below and staminate flowers above. In the highest sedges like Carex lupulina Muhl. the monosporangiate flowers are on separate spikelets, the staminate spikelets above, the carpellate spikelets below. In Carex, therefore, we approach the condition present in Indian corn.

What is the nature and cause of this progressive change in the area of the tissue involved? In the first case mentioned above, the differentiation takes place in the sporophylls on the same floral axis; in the second case the floral axes produce each but one kind of sporophylls, but the two kinds of flowers are on the same inflorescence axis; in the third case an entire spikelet or group of spikelets is similarly affected. The whole matter can only be interpreted, if at all, by a study of the evolutionary series of expressions in related species. Isolated studies do not give a true picture; in fact do not present the problem. But in no study could the phenomena of segregating or associating chromosomes be involved but the much more difficult problem of changing hereditary expressions and states in a common vegetative tissue.

As an example of the changes of morphological expression that take place in a growing bud, an ordinary grass may be considered, like Bromus secalinus L. The grasses are derived from plants whose buds produced three spirals of leaves in the vegetative parts as well as in the flower, the ancestral flower

being a trimerous, pentacyclic structure. In the sedges the leaves are still in three spirals, but in the grasses they are in two; in other words, the leaves of the grasses are two-ranked. During the vegetative growth of Bromus, therefore, its bud gives off alternately incepts of leaves on opposite sides of the stem. These leaves are differentiated through the activity of hereditary units into the form characteristic of the species. This two-ranked arrangement is a culmination type of morphological expression. As stated, the species evolved from ancestors in which three spiral incepts were successfully organized instead of two. Now the cells of the terminal bud actually contain the hereditary ability to develop threes as will appear below. But for some cause the ability is suppressed. The bud, using a metaphor, dances a two-step instead of a waltz. When a spikelet begins to develop, the two-ranked condition continues and the two-ranked empty glumes are produced and a number of flowers, also in two ranks. The flower bud on the spikelet also produces two-ranked glumes, the flowering glumes, unless the palet represents more than one leaf. But the first set of floral organs proper, the lodicules are produced in a three spiral arrangement. The third, or posterior one, however, is suppressed in harmony with the bilateral nature of the evolved plant. One step down in the evolutionary scale, in the bamboo tribe, the third lodicule is present in the proper position as it should be in a monocotyl flower. In some way the bilateral nature does not act so intensely as in Bromus and the higher grasses in general. The lodicules probably represent a corolla, the calyx being suppressed. Next the flower bud of Bromus not only develops three incepts in typical tripartite arrangement, alternate with the lodicules, but these organs pass into that strange state which determines the nature of stamens and male gametophytes with male cells or sperms as the final goal. Now all of this up to the formation of microsporocytes is a matter of vegetative growth. The cells in the stamens have received the same heredity as those which produced leaves, glumes, or lodicules. The three stamens are the only structures which show the typical ancestral morphology in the entire life cycle of the grass under consideration. Next the bud fails to perform and the second, expected set of three stamens does not develop. In many bamboos all the six stamens are present, as in any typical monocotyl that is not specialized too much.

Finally the bud does another "three-step" forming a united tricarpellary gynecium, but here again the third stigma on the outside in the bilateral plane is suppressed. All three stigmas are usually present in Arundinaria and other bamboos. At the same time the incept of the gynecium has set up in its cells a sexual state just the opposite from that of the andrecium immediately below although so far as any one knows and so far as the evidence goes these cells have received exactly the same hereditary units as have those of the leaves, the glumes, the lodicules, and the stamens. But in some way a new physiological state has been established which causes the heredity to give rise to a new morphological expression along with femaleness.

At each whorl there is a difference in hereditary expression, a change in the activity and latency of numerous hereditary factors. This change in activity and latency, the writer believes is due to changes in physiological state of the tissues involved, whether chemical or otherwise. The progressive changes of morphological expression in a vegetative tissue do not find their explanation in any Mendelian formulæ. Mendelian ratios, segregations and associations have no direct bearing on the problem. Just as these profound changes in the vegetative development are brought about by some state in the cells which influence the hereditary activity, so essentially similar changes in physiological activity bring about sexual expressions, causing the cells or tissues to give rise to male or female morphological structures with their accompanying sexual activities.

It may be that in some cases physiological states or hereditary factors may arise in an allosome or special chromosome which may assist in retaining and intensifying a male or female state already established, but so far as the writer can see the animal kingdom presents the same problems of changes in sexual states in common tissues as does the plant kingdom. The lower animals are hermaphrodites and the higher unisexual forms are after all only modified hermaphrodites. Sex-limited and sex-linked transmission can readily be explained without postulating a sex-determining allosome, with no more complexity of hypotheses than if such mendelizing units are assumed. And it must always be kept in mind that with the assumption of sex-determining chromosomes the greater

part of sexual phenomena becomes unexplainable and contradictory. The presence of allosome difference in certain sexual individuals does not make it necessary for us to amend the proposition that sexuality either male or female is a state or condition and not a mendelian factor or set of factors.

For the convenience of those who wish to make a study of our more common or interesting species, the following short list is given as an index to the general condition usually present in monecious and diecious plants:

Four genera to illustrate the relation of diecious to bisporangiate species—Thalictrum, Rumex, Acer, Fraxinus.

Thalictrum clavatum DC. Flowers bisporangiate.

Thalictrum dasycarpum Fisch. & Lall. All gradations of bisporangiate to staminate and carpellate flowers on the same plant.

Thalictrum dioicum L. Plants diecious.

Rumex crispus L. With bisporangiate flowers and carpellate flowers containing prominent vestigial stamens on the same plant. The stigmas are much branched.

Rumex altissimus Wood. Monecious. The carpellate flowers have six vestigial stamens; the staminate flowers have a vestigial gynecium with three slightly branched stigmas.

Rumex acetocella L. Diecious. The staminate flower has a minute vestigial gynecium with three, unbranched, vestigial stigmas; the carpellate flower apparently has no vestigial stamens; the stigmas are much branched.

Acer platanoides L. Imperfectly diecious. Some carpellate trees have staminate and some staminate trees carpellate flowers; both kinds of flowers have prominent vestiges of the opposite organs. The flowers have large petals and a prominent nectar disk.

Acer saccharinum L. Diecious. Carpellate flowers with vestiges of stamens; staminate flowers with vestigial gynecia. Some plants occasionally have bisporangiate flowers. The petals are absent.

Acer negundo L. Strictly diecious. The flowers are much reduced and have no vestiges of the opposite organs.

Fraxinus cuspidata Torr. Flowers bisporangiate with a calyx and corolla; very fragrant.

Fraxinus americana L. Strictly diecious. Flowers small without corolla but with a small calyx; no vestiges of the opposite sporophylls.

List of a few monecious and diecious species with notes on the condition of the reciprocal organs in the two types of flowers:

Sagittaria latifolia Willd. Monecious, occasionally diecious. The staminate flower has prominent vestigial carpels, only slightly different from the fertile carpels of the carpellate flower. The carpellate flower has minute vestiges which, no doubt, represent stamens.

Sagittaria rigida Pursh. Monecious. The condition of the flowers is the same as in S. latifolia.

Phoenix dactylifera L. The carpellate flower has six vestigial stamens; the staminate flower has three vestigial carpels.

Cocos nucifera L. Monecious. The carpellate flower has six minute vestigial stamens, one or more of which occasionally develop nearly normal anthers; the staminate flower has three prominent, only slightly united, vestigial carpels.

Typha latifolia L. Monecious. The flowers are much reduced and neither type shows any vestiges of the opposite organs. More primitive related genera, belonging to the Pandanaceæ, show vestigial structures.

Arisæma triphyllum (L.) Torr. More commonly diecious. Spadixes occur which have only carpellate flowers; some have carpellate flowers with a few imperfect staminate flowers at the top; some have normal carpellate flowers below and normal staminate flowers above; some are almost entirely staminate with two or three normal carpellate flowers situated in about the middle of the spadix; and some are entirely staminate.

Panicum virgatum L. Each spikelet contains a bisporangiate and a staminate flower.

Zizania aquatica L. Monecious; with staminate spikelets below and carpellate spikelets above, on the inflorescence; the carpellate spikelet contains six vestigial stamens; the staminate spikelet contains a vestigial gynecium. In the transition tissue there are normal, bisporangiate spikelets. The awns are sex-limited, depending on the degree of the carpellate condition.

Andropogon furcatus Muhl. In each pair of spikelets, the sessile spikelet is bisporangiate; the stalked spikelet is staminate with a vestigial gynecium.

Tripsacum dactyloides L. Monecious; with the carpellate spikelets below and the staminate above. The carpellate flower with three vestigial stamens; the staminate flower with a vestigial gynecium.

Smilax hispida Muhl. Diecious. The carpellate flower has six vestigial stamens; the staminate flower contains no vestige of the gynecium.

Dioscorea villosa L. Diecious. The carpellate and staminate flowers contain vestiges.

Thalyctrum dasycarpum Fisch. & Lall. On the same plant may be found purely carpellate flowers, purely staminate flowers, carpellate flowers with one stamen, staminate flowers with one carpel, and all gradations between, some flowers having about half of each kind of organs. Some species of Thalictrum are diecious.

Menispermum canadense L. Diecious. The carpellate flower has about twelve vestigial stamens; the staminate flower has no vestiges.

Sassafras sassafras (L.) Karst. Diecious. The staminate flower has a vestigial carpel; the carpellate flower has six staminodes.

Zanthoxylum americanum Mill. Usually diecious. The staminate flower has prominent vestigial carpels, the carpellate flower sometimes has minute vestigial stamens.

Ptelia trifoliata L. Imperfectly monosporangiate and imprefectly monecious. The staminate flower has a prominent imperfect gynecium; the carpellate flower has five vestigial stamens.

Ailanthus glandulosa Desf. Diecious. The carpellate flower has ten prominent staminodes; the staminate flower has a prominent vestigial gynecium of five carpels.

Napea dioica L. Diecious. The carpellate flower has a vestigial stamen column; the staminate flower has no vestige.

Rumex acetosella L. Diecious. The staminate flower has a small vestigial gynecium with three minute stigmas; the carpellate flower has no vestiges.

Aruncus aruncus (L.) Karst. Diecious. The carpellate flower has vestigial stamens; the staminate flower has three vestigial carpels.

Gymnocladus dioica (L.) Koch. Diecious. The carpellate flower has ten large staminodes; the staminate flower has a vestigial carpel.

Acer negundo L. Apparently strictly diecious with no vestiges of the opposite organs. In the lower species of Maples the trees are imperfectly diecious and the flowers have very prominent vestiges of the opposite organs.

Morus rubra L. Diecious. Staminate flowers with a vestigial gynecium; carpellate flowers without vestiges. Often there are staminate and carpellate catkins on the same tree; sometimes there are carpellate and staminate flowers on the same catkin; sometimes a carpellate catkin may contain a single staminate flower.

Cannabis sativa L. Diecious; but the plants are of various degrees; some carpellate plants may have stamens and staminate plants may have carpels.

Populus deltoides Marsh. Apparently strictly diecious, as also some willows, but there are intermediate willows, occasionally.

Cucumis sativus L. Monecious. The carpellate flower has three vestigial stamens; the staminate flower has a tricarpellate, vestigial gynecium.

Diospyros virginiana L. Usually diecious. Carpellate flower with vestigial stamens; staminate flower with a large vestigial gynecium.

Fraxinus americana L. Apparently strictly diecious. Various species of Fraxinus present gradations from bisporangiate, conspicuous flowers to diecious flowers with loss of perianth and nectar glands.

Ambrosia trifida L. Monecious. The staminate flower has a vestigial gynecium; the carpellate flower shows no vestiges of stamens.